

Functional Morphology of the Abdomen and Phylogeny of Chrysidid Wasps (Hymenoptera: Chrysididae)

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Abstract.—The wasp family Chrysididae is characterized in part by the loss of a functional sting, and the internalization of 2 or more abdominal segments. These segments are telescoped within the abdomen and function as an independently muscled ovipositor or genital tube. Accompanying this internalization are shifts in the position of the major muscles involved in pronation, retraction and protraction of the segments from that of the typical ground plan seen in other stinging wasps. There is also an accompanying loss of musculature on the remaining external segments. The degree of modification and internalization correlates with the type of host parasitized, with the least in Cleptinae (parasites of prepupal sawflies), and the most modification in Chrysidinae (nest parasites of bees and wasps). Phylogenetic relationships among chrysidid subfamilies can be traced using derived features of structural and muscular changes in the abdomen. In addition, these modifications reflect compromises between oviposition, copulation and defense.

There are few studies of insects in which attempts are made to explore the function of structural features commonly used in systematics to demonstrate phylogenetic relationships. Within Hymenoptera the structure and function of the ovipositor has been examined in some detail (Austin 1983, Austin and Browning 1981, Copland and King 1971, Oeser 1961, Robertson 1968, Scudder 1961).

Unfortunately, in many insect groups neither the systematics nor the biology are sufficiently well understood to permit the examination of relationships between structural modifications and hosts, or other aspects of the biology. The family Chrysididae is one exception to this problem. The family has just been revised on a world basis, with detailed analysis of phylogenetic relationships (Kimsey and Bohart 1991), and at least general categories of hosts are known for tribes and subfamilies. There appear to be strong correlations in this family between the type of host and modifications of the chrysidid abdomen, in both sexes. These changes in external and internal morphology of the chrysidid abdomen support relationships discussed previously (Bohart and Kimsey 1982, Kimsey and Bohart 1991).

In the vast majority of aculeate, or "stinging", wasps the ovipositor functions as both a defensive and an offensive structure, used to inject prey or potential predators with venom. This sting apparatus has been secondarily lost or highly reduced in several groups, including the stingless bees

(Meliponini, Apidae), a number of ant taxa, and Chrysididae. In all but the last group the apparent abdomen is otherwise relatively unmodified, with 6 external segments in females and 7 in males, excluding the propodeum, and the sting apparatus involves segments VIII and IX. The male genital capsule is internally subtended by gastral segment IX. The structure of the sting and male terminalia have been studied in detail by Carpenter (1986), Oeser (1961), Rasnitsyn (1980) and Snodgrass (1942) among others.

However, within the family Chrysididae radical changes in the abdomen of both males and females have occurred. In this group the sting is considerably reduced and functions more as an egg guide than in any defensive manner, and both the male and female genitalia are subtended by an eversible tube formed by 2 or more internalized abdominal segments.

Somewhere in the transition from some ancestral form to the Chrysididae the 2 apical external abdominal segments (VI and VII in females, and VII and VIII in males) were internalized, resulting in a primitive ground-plan of 5 external segments in males and 4 in females; a condition found in Cleptinae, Amiseginae and Loboscelidiinae. Although this ground-plan of 5 external abdominal segments is primitive for chrysidids, it is apomorphic within the Aculeata. This basic modification of the abdomen in turn facilitated a series of specializations that are unique to this family,

which reflect various compromises between oviposition, copulation and defense.

MATERIALS AND METHODS

This study is based on morphological studies of the family Chrysididae. External morphology of more than 2000 species of Chrysididae was examined for a monograph of the family (Kimsey and Bohart 1991). Internal anatomy was studied in dissections of preserved material representing several aculeate families, and subfamily groupings within the Chrysididae (Table 1).

Table 1. Taxa dissected for studies of abdominal musculature. The sex of specimens examined is given in parentheses, M = male, F = female.

Family	Subfamily	Species
Chrysididae	Chrysidinae	<i>Chrysis nitidula</i> (Fab.) M, F
		<i>Chrysis</i> sp. M
		<i>Chrysurissa densa</i> (Cr.) M, F
		<i>Chrysuria</i> sp. (f)
		<i>Hedychrum</i> sp. M, F
	Cleptinae	<i>Cleptes alienus</i> Patton M
		<i>Cleptes semiauratus</i> (L.) F
		<i>Adelphes anisomorphae</i> Kr. M, F
	Amiseginae	<i>Rhabdopyris</i> sp. M, F
		<i>Auplopus</i> sp. M
Bethylidae		<i>Apis mellifera</i> L. F
Pompilidae		
Apidae		

The muscle arrangements found in *Rhabdopyris* (Bethylidae), *Auplopus* (Pompilidae) and *Apis* (Apidae) all closely resembled one another (as in Fig. 1). Therefore, the condition found in these taxa was used as the primitive ground plan against which the muscle positions in chrysidids were compared (Figs. 2-4).

These specimens were fixed in solutions using formalin-acetic acid (FAA). Unfortunately, I could only obtain specimens of *Adelphes* and *Rhabdopyris* preserved directly in 70% ethanol, without an interim fixative. The relatively poor state of preservation of these specimens made it impossible to determine muscle attachments in the ultimate and penultimate abdominal segments, those directly involved with the sting and genital capsule.

Although the chrysidid abdomen is quite modified, homologies can be seen between the musculature in this family and that of other aculeates. There have been few published studies of the abdominal musculature of Aculeata (Duncan 1939, Snodgrass 1942). As a result, I am using the terminology for the musculature of Snodgrass (1942) where possible, to aid in comparisons (Table

Table 2. Terminology taken from Snodgrass (1942) and code numbers used in Figs. 1-4 for muscles of the apparent abdomen, beginning at the petiole.

- 1s—*Median Intersegmental Ventral Muscle of Metathorax*. This is the primary depressor of the abdomen, originating on the metasternum and attaching on sternum II (Snodgrass No. 118).
- 2s—*Oblique Internal Ventral Muscle of Segment III*. This muscle originates near the midline of segment III and attaches on the anterior apodeme of segment IV. It was found only in Chrysidinae. There is no clearly homologous muscle in the honeybee or other aculeates. It may be derived from 3s as that muscle has the same point of insertion.
- 3s—*Lateral Internal Ventral Muscle*. This muscle originates adjacent to the anterior sternal apodeme of the anterior sternum, and attaches on anterior apodeme of the posterior sternum (Snodgrass Nos. 131, 142, 153, 164, 175).
- 4s—*Medial Internal Ventral Muscle*. Originates on the apical margin of the anterior sternum, and attaches on anterior margin of the posterior sternum (Snodgrass Nos. 130, 141, 152, 163, 174).
- 5s—*External Ventral Muscle*. This muscle originates basally on the anterior sternum and attaches on the apodeme of the posterior sternum (Snodgrass Nos. 135, 146, 157, 168).
- 1t—*Medial Internal Dorsal Muscle*. This muscle originates posterior to the anterior apodeme of the anterior tergum, and attaches apicomediaally on the posterior tergum (Snodgrass Nos. 124, 133, 144, 155, 166).
- 2t—*Lateral Internal Dorsal Muscle*. This muscle originates posterior to the apodeme of the anterior tergum, and attaches laterally on the posterior tergum (Snodgrass Nos. 125, 134, 145, 156, 167).
- 3t—*External Dorsal Muscle*. This muscle originates posterolaterally on the anterior tergum, and inserts on the anterior apodeme of the posterior tergum (Snodgrass Nos. 135, 146, 157, 168).
- 1ts—*Lateral Muscle of Tergum II*. This muscle originates on the dorsal surface of the tergum, and attaches on the anterior margin of the sternum (Snodgrass No. 129).
- 2ts—*First Lateral Muscle*. This muscle originates posterolaterally on the tergum, and extends apicolaterally between sternum and tergum, attaching below the anterior apodeme of the sternum (Snodgrass Nos. 138, 149, 160, 171).
- 3ts—*Second Lateral Muscle*. This muscle originates laterally on the sternum, and inserts laterally on the tergum (Snodgrass Nos. 13, 9, 150, 161, 172).

2). Homologies were determined by the position of the muscle insertions, and the assumption that a shift in position was more likely than derivation of an entirely new muscle. The insertion was assumed to be the narrowest part of the muscle, often with a distinct tendon. This is not always easy to determine in Snodgrass' illustrations.

Phylogenetic analysis of the resulting data set was done with the program Hennig-86 of Farris.

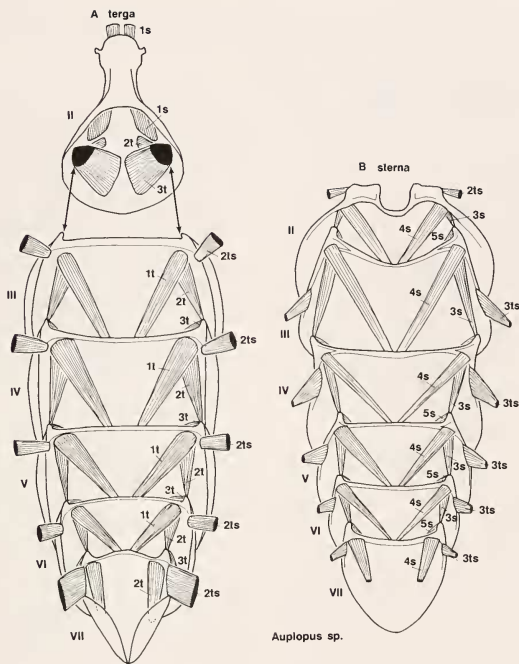


Fig. 1. *Auplopus* sp., male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

RESULTS

Nonchrysidid Abdomen

The abdominal musculature of the external abdominal segments appears to be fairly consistent when comparisons are made among distantly related families. The typical configuration can be seen in Fig. 1. The basic muscle pattern is repeated from one segment to the next, except in the first and last external segments. There are basically 3 sternal, 3 tergal and 3 tergosternal muscle pairs in each intermediate segment. The primary intersegmental muscles, 3s, 4s, 1t and 2t form a V-shaped con-

figuration in the 3 nonchrysidid species examined (as in Fig. 1).

Chrysidid Abdomen

Although homologies can be seen between the musculature of the chrysidid abdomen and that of other aculeates, there are a considerable number of variations in muscle positions and development between the two as well as among the chrysidid subfamilies (Tables 2-3).

The significance of one difference in the musculature of segment II between the Chrysididae and other Aculeata examined is unclear. In other

Table 3. A comparison of the presence or absence of specific muscles in 3 chrysidid subfamilies and the pompilid *Auplopus*. The muscle numbers correspond with those given in Table 2.

Segment No. and Muscle	<i>Auplopus</i>	Cleptinae	Amiseginae	Chrysidinae
II 1ts	+	+	+	+
2ts	+	0	0	0
3ts	0	+	+	+
1t	+	+	0	0
3t	+	+	+	+
3s	+	+	0	0
4s	+	+	0	+
5s	+	+	+	+
III 2ts	+	+	+	0
3ts	+	+	+	+
1t	+	+	+	+
2t	+	+	+	0
3t	+	+	+	+
2s	0	0	0	+
3s	+	+	+	+
4s	+	+	+	+
5s	+	+	+	+
IV 2ts	+	+	+	0
3ts	+	+	+	+
1t	+	+	+	+
2t	+	+	+	0
3t	+	+	+	+
3s	+	+	+	+
4s	+	+	+	0
5s	+	+	+	+
V 2ts	+	+	+	0
3ts	+	+	+	+
1t	+	+	0	+
2t	+	+	+	0
3t	+	+	+	+
3s	+	+	+	+
4s	+	+	+	0
5s	+	+	+	+
VI 2ts	+	+	+	+
3ts	+	+	+	+
1t	+	+	0	+
2t	+	+	+	+
3t	+	+	+	+
3s	+	+	0	+
4s	+	+	0	0
5s	+	+	+	+

aculeates sternum II has one tergo-sternal muscle pair inserting on the anterior apodeme. Thus it is labeled 2ts in Fig. 1B. In chrysidids there is only one tergo-sternal muscle pair on segment II but since this is located laterally near the middle of the plate it is labeled 3ts. Superficially this appears to be a major difference between the two groups, but in fact may be a shift in the position of 2ts in chrysidids.

Cladistic analysis of the data set generated by muscle traits found in the chrysidid and

nonchrysidid taxa, using the Hennig-86 program of Farris, resulted in a CI of 100 and RI of 100.

MORPHOLOGY

Cleptinae.—The external gastral segments are unspecialized; males have 5 segments and females 4. These external segments are freely articulated and well muscled. The remaining abdominal segments form an ovipositor or genital tube from segments VI-VIII (females) or VII-IX (males), which is held telescoped within the abdomen.

The internal segments VI or VII-IX are not particularly differentiated from the external ones. They differ primarily in the absence of the distinctive lateral tergal lobe seen on the external segments. Terga II-V or VI have a large lateral lobe, the laterotergite, set off from the rest of the tergum by a faint weakening apically and by the position of the spiracle. This lobe covers a large part of the sternum.

Cleptines have largely retained the V-shaped configuration of 1t and 2t, and 3s and 4s, typical of other aculeates (Fig. 2). These 4 muscle pairs are also well developed. However, 1t and 2t have anteriorly shifted away from the anterior apodeme and have assumed a more medial position.

Amiseginae.—As in cleptines the external abdomen consists of 5 segments in males and 4 in females. However, in this group the intersegmental musculature and configuration of the terga has been considerably modified (Fig. 3). The invaginated segments VI or VII-VIII are greatly reduced, with VIII represented by linear, almost membranous flaps. In addition, terga II and III cannot be moved independently and appear to be closely articulated or fused. No indication of the presence of 1t or 2t could be found between these two segments.

There are also other differences on segments III-VI. Muscles 1t and 4s are very slender, and are located nearly parallel with the midline of the plate. 2t and 3s are short and originate away from the anterior apodeme, often toward the midline of the segment.

Unlike the Cleptinae, terga II-IV or V have the laterotergite clearly delimited by a sulcus extending from the anterior to the posterior tergal margin. The spiracle is located just ventrad of this sulcus. This tergal sulcus forms a midline extending the length of the abdomen when it is viewed in profile.

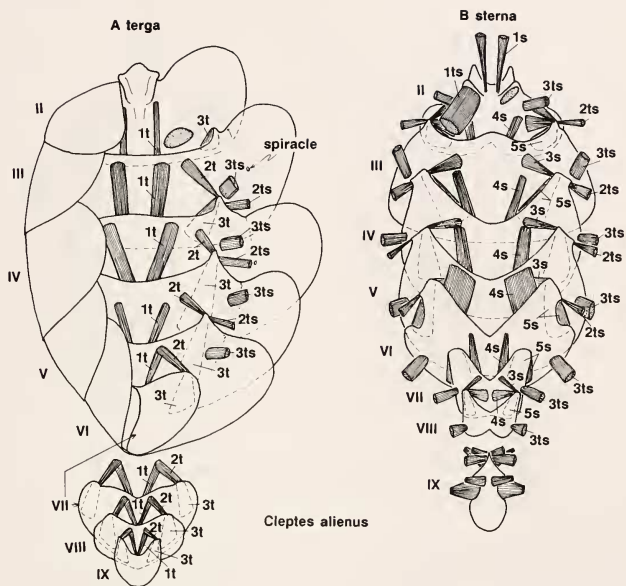


Fig. 2. *Cleptes alienus*, male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

The terga and sterna are both convex in this subfamily.

The reduced internal segments result in a different configuration of the ovipositor and genital tube as compared with other chrysidids. In females, segments VI–VIII form a sheath around the elongate sting elements, rather than a separate eversible tube basad of the sting elements. Segments VII–IX are also reduced in males, and form a short, simple pregenital element at the base of the genital capsule.

Based on dissections of dried specimens of *Loboscelidia* (Loboscelidiinae), and the descriptions of Day (1978), the structure of the abdominal terga and sterna are nearly identical to those in Amiseginae. The abdominal musculature in loboscelidiines probably closely resembles that of amisegines.

Chrysidinae.—The number of external gastral segments is reduced to 4 or fewer in males and 3 or fewer in females, depending on the tribe. Parnopines are the least reduced with 4 in males and 3 in females (Telford 1964). Elampines and chrysidines have 3 in both sexes, and allocoeliines have 2 in both sexes, with the sternum of segment IV still largely exposed.

The musculature is considerably modified on these external segments (Fig. 4). As in Amiseginae the tergum is sharply divided into a primary tergite and secondary laterotergite by a sulcus. The spiracle may be located near the sulcus on the primary tergite or on the laterotergite. The sterna are narrowed and the laterotergite sharply bent ventrad, forming part of the apparent sternum. The juncture between the primary tergite and laterotergite is

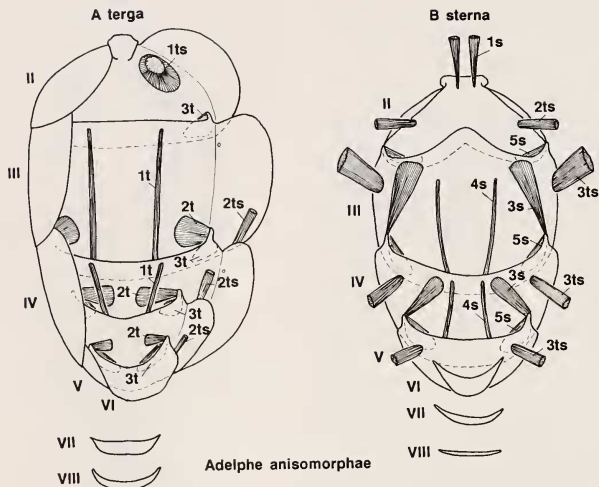


Fig. 3. *Adelphoanisomorpha*, male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

sharply folded. The resulting sternum is flat or concave, giving the gaster a cuplike appearance. The internalized segments are highly modified in chrysidines. However, they have all retained the basic musculature found on these segments in other aculeates.

In addition, chrysidines can roll up in a tight ball when disturbed. Several structural changes allow this posture. The region around the petiolar articulation between the propodeum and first gastral segment has become modified, allowing the abdomen to be rotated up against the thoracic venter. The petiolar socket is broader in chrysidines, the hindcoxal articulations are oriented in a more horizontal position than in cleptines, and the upper surface of the hindcoxae is flattened, allowing the abdomen to rotate anteroventrally and cover the legs and thoracic venter. When the abdomen is curled up against the head and thorax only the top of the eyes, the upper one-third of the thorax and the femorotibial articulations of the legs are visible (Fig. 5b).

The arrangement of muscles in the Chrysidinae

differs considerably from that of other chrysidids as well as other aculeates, although it more closely resembles the pattern seen in Amiseginae than any other taxa (Table 3). There are 2 sternal muscles (Fig. 4B) on segments III and IV, which differ in position from that seen in the other taxa examined. These are labeled 4s and 2s respectively. Muscle 4s has a similar attachment and insertion as 4s in other chrysidids. Muscle 2s does not appear to be homologous with any muscle seen in the aculeate ground plan, although the insertion of this muscle on the anterolateral apodeme suggests that it may be derived from 3s. However, contraction of both of these muscles would not only pull the sternal plate anteriorly but would also bend the plates involved, increasing the convexity of the abdominal sternum.

There are other differences in musculature as well. Segments III-V lack 2t and 2ts, and segments IV-VI lack 4s. Finally, segment III lacks 2s.

Segment IV is the most highly modified in Chrysidini where the origin of 3t, the primary protractor of the internal segments, is marked by

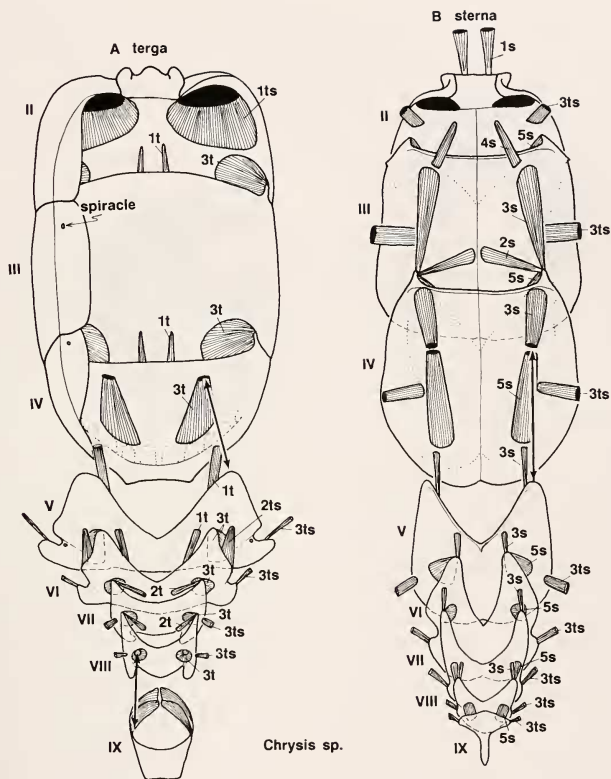


Fig. 4. *Chrysis* sp., male, terga (A), sterna (B). Letters refer to muscles given in Table 2. Roman numerals indicate segment numbers. Dashed lines indicate tergal, sternal and muscle margins covered by an adjacent plate.

the anterior margin of the pit row (Fig. 4A), a row of ovoid depressions near the apical margin of the tergum. Segments V-VIII are differently shaped than the external segments, having strong anterolateral lobes on both the terga and sterna.

DISCUSSION

The internalization of abdominal segments allowed the chrysidids to develop a highly mobile and independently muscled ovipositor or genital tube. Several concurrent modifications are involved. The internalized segments retained their intersegmental musculature, with the associated

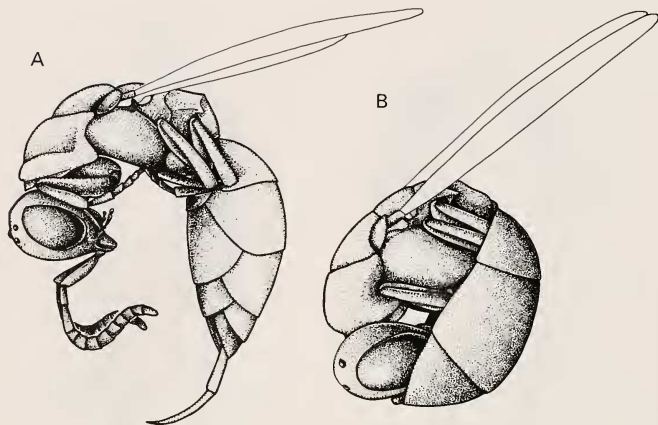


Fig. 5. Defensive posture of *Cleptes alienus* (A) and *Hedychrum* sp. (B).

enlargement of the tergal, sternal and tergo-sternal muscles, particularly 3t, 4s, 5s and 3ts. The intersegmental muscles, 3t, 5s and 4s, between the apical external segment and basal internal segment, serve as basal protractors and retractors of the tube. These are shifted in position and enlarged as shown in Fig. 4, where the origin of the major tergal protractor muscle, 3t, on tergum IV is situated submedially near the posterior margin of the tergum, and the muscle itself is elongate anteriorly. Contraction of this muscle pulls the anterior margin of tergum V nearly even with the posterior margin of IV. Relaxation of this muscle and contraction of 1t pulls the anterior apodemes of tergum V anteriorly, and nearly even with the anterior margin of IV. Muscle 5s on the sternum functions similarly. Therefore, exertion of the abdominal tube is primarily accomplished by contraction of 3t and 5s. The tube is telescoped within the abdomen at rest by contraction of 3s, 4s, 1t and 2t. In addition, retention of the intersegmental muscles on the tube segments enabled it to be flexible and mobile. The external segments have retained remnants of intersegmental muscles but these muscles are considerably reduced or lost in the case of those that function as tergal retractors (1t) and pronators (5s), or greatly enlarged as in the muscle that holds the

anterior tergal apodeme of a posterior segment to the side of the anterior tergum (3t), resulting in an almost complete loss of flexibility in the external segments in the Chrysidinae. Muscle 3t has a dual function in the Amiseginae and Chrysidinae. On the external segments 3t is very short and actually serves to limit movement between these segments. This muscle serves as one of the primary protractors of the internal segments and between these and the apical external segment.

Retracting the apical abdominal segments within the abdomen necessitated a change in the position of the muscle attachments between the apical external and basal internal segments. In chrysidids this muscle attachment has shifted from the base of the apical external segment to a submedial placement. Retraction is accomplished by contraction of 3s, 4s, 1t and 2t. In other aculeates these muscles (3s, 4s, 1t and 2t) serve to hold the abdominal segments tightly together and enable lateral, dorsal or ventral pronation, or allow limited posterior extension or elongation (3t and 5s).

The degree of modification of the intersegmental musculature varies from subfamily to subfamily, with the least occurring in the Cleptinae, and the greatest in Chrysidinae. The result is that in the Chrysidinae, where the largest number of seg-

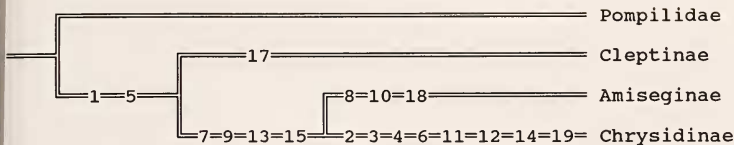


Fig. 6. Phylogenetic tree showing relationships of chrysidid subfamilies, using features of the abdomen and hosts. Numbers refer to derived characters given below. 1, Abdominal segments VI-VIII (females) or VII-IX (males) internalized. 2, Abdominal segments V (females) or VI (males) also internalized. 3, Segment III with muscle 2s. 4, Segments III-V without 2t. 5, Segment II without 2ts. 6, Segments III-V without 2ts. 7, Segment II without 1t. 8, Segments V-VI without 1t. 9, Segments II and VI without 3s. 10, Segment II without 4s. 11, Segments IV-VI without 4s. 12, Segment III with 2s. 13, Muscles 1t and 2t, and 3s and 4s not forming V-shaped configuration. 14, Abdominal venter flat or concave. 15, Terga with laterotergite separated by complete sulcus. 16, Segments VIII and IX extremely reduced, linear. 17, Parasites of sawfly prepupae. 18, Parasites of wasps and bees.

ments are invaginated, the external abdomen is almost completely inflexible.

In Cleptinae the internal segments are not strongly differentiated from the external segments. The resulting ovipositor tube is robust and long, and the external abdomen retains some flexibility. These wasps parasitize prepupal sawfly larvae, ovipositing through a hole opened in the host cocoon, which is often located in soil or leaf litter.

In Amiseginae and Loboscelidiinae the intersegmental muscles are reduced on the external segments. The internal segments are also reduced, resulting in a needlelike ovipositor or short pregenital ring. These wasps parasitize walking stick eggs that are singly broadcast, and have a thick chorion. They initially open the egg by nipping a small hole in the chorion, using the ovipositor to place an egg in the phasmatid egg (Costa Lima 1936, Krombein 1983).

The greatest degree of modification has occurred in the Chrysidinae. These wasps are primarily nest parasites of wasps and bees, and will enter a nest whether the adult host is present or not. As a result, a third component, protection from attacks by the host, is involved in the abdominal modification of this group. Therefore, in this subfamily these modifications represent compromises between oviposition, copulation and defense. The chrysidid wasp rolls up in a ball and the inflexible cuplike external abdomen is used as a protective shield covering the appendages. The internalized, intermusculated segments provide the flexibility needed for oviposition and copulation, while being retractable and therefore not vulnerable to damage by the adult host.

Some use has been made of the shape of the sternal plates in phylogenetic discussions of the relationships of the families placed in the Chryridoidea. Rasnitsyn (1980, 1988) used the shape of sternum II and how it joined III as one of several characters to demonstrate the close relationship among Chrysididae, Bethyliidae and Embolemidae. However, his assumptions about the morphology of sternum II appear to be misinterpretations of the structure of this plate. Based on the position of muscles on sternum II this plate is not secondarily expanded into "paired membranous lobules overlapping the base of III". There is no indication internally of a butt-joined articulation between sternum II and III. The butt-joined articulation between these sterna is more clearly an apomorphy for Bethyliidae. The validity of this character was first called into question by Carpenter (1986).

These changes in abdominal morphology can be used to demonstrate the phylogenetic relationships among the chrysidid subfamilies (Fig. 6). In fact there is no homoplasy in these musculature traits. When this data is analyzed the resulting cladogram is identical to those produced using strictly external morphological characteristics (Bohart and Kimsey 1982, Kimsey and Bohart 1991).

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